DISJUNCTION OF GREAT BASIN PLANTS IN THE NORTHERN SIERRA NEVADA

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The montane zone of the Sierra Nevada is rich in number and diversity of floristic elements. Taxa that have had different geographical origins and migrational histories are found within adjacent communities. Many subalpine and alpine taxa in the Sierra show their closest relationships to floras of the cool, mesic areas of the Cascades and Rocky Mountains (Sharsmith, 1940; Smiley, 1915; Pemble, 1970); others are related to the warm, dry areas of adjacent lowlands (Chabot and Billings, 1972; Went, 1948).

Klyver (1931), Major and Bamberg (1963), Neilson (1971), and Smith (1973) noted typically Great Basin taxa in xeric sites west of the crest of the Sierra Nevada. These taxa often are disjunct by considerable distances from their nearest occurrences to the east, being separated by expanses of mesic forest vegetation.

At Carson Pass, Alpine County, California, dry site vegetation is strikingly similar to that occupying upland sites throughout much of Nevada. This similarity will be described and discussed in relation to past environmental conditions that may have been responsible for the migration and subsequent disjunction of the Great Basin floristic element on the crest and west slope of the northern Sierra Nevada and in cismontane California in general.

CARSON PASS

Carson Pass lies astride the crest of the Sierra Nevada. Several high peaks in the Carson Range exceed 3000 m elevation at Carson Pass: Steven's Peak (3064 m), Red Lake Peak (3066 m) and Round Top (3163 m). Carson Pass is located in the low saddle between the two last-named peaks at 2612 m. Immediately to the east is Hope Valley, a broad, lowland basin at 2000–2100 m, then another ridge rising to above 3000 m. This ridge is cut by the canyon of the West Fork of the Carson River to the level of Hope Valley and leads to the floor of the Great Basin to the east. North of Carson Pass on the east side of the crest lies Lake Tahoe at 1930 m, separated from Carson Pass by ridges rising to 2850 m.

Climatically, the region is typical of subalpine localities on the west slope of the Sierra Nevada, but records are scanty.

Geologically, the Carson Pass area is quite complex. Intrusive granitic and extrusive volcanic rocks compose the majority of the substrates.

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There are small exposures of intrusive volcanic and metasedimentary formations. Metamorphism has altered many of the regional formations (Crawford, 1969). Moderate folding and faulting have placed contrasting substrates in juxtaposition.

Vegetation types found at Carson Pass are typical of timberline elevations in the Sierra. Open forests of *Pinus albicaulis,* denser forests of *Abies magnifica, Tsuga mertensiana,* and *Pinus monticola,* mesic meadow, and alpine associations form a complex mosiac. Xeric areas of considerable extent occur chiefly on southerly exposures underlain by Miocene and Pliocene andesitic mudflow breccias.

Disjunct Taxa

The flora of the subalpine and alpine zone at Carson Pass is diverse: 580 taxa of vascular plants have been collected from above the 2440 m contour within a radius of 10 km (Taylor, 1974). The total flora of the area shows high overall similarity to those of nearby regions, such as the Lake Tahoe basin (Smith, 1973) or Tuolumne Meadows (Howell, 1944; Clausen, 1969; Pemble, 1970). However, there is a sizable Great Basin floristic element at Carson Pass that is not as well developed in the above locations or other areas in the Sierra for which plant lists are available (e.g., Norden: Howell, 1943; Convict Creek basin: Major, 1966; Pemble, 1970; Rock Creek Lake Basin: Peirson, 1938, 1942; Mineral King: Howell, 1952; Rice, 1969).

Fifty-six disjunct taxa (Table 1) characteristic of the semiarid shrub-steppe and pinyon woodland associations of the Great Basin can be considered to compose the nucleus of this disjunct element. All have the major part of their distribution in the Great Basin province (Fenneman, 1928). Vouchers are deposited in DAV or CAS; collection information and nomenclature can be obtained from Smith (1973) and Taylor (1974).

Some of the taxa in Table 1 are elevationally disjunct by as much as 1000 m above their nearest populations 20 km to the east. Several others have more notable disjunctions.

Betula occidentalis: The nearest populations to the Woods Lake locality at Carson Pass (Smith, 1973) are about 200 km to the south in the Owens Valley, Inyo County (Davidson, 1911; Griffin and Critchfield, 1972) and at mid-elevations in the upper drainages of the Kings and Kern rivers in the southern portion of the Sierra (Rockwell and Stocking, 1969) and 250 km northeast on the uplands surrounding Mt. Shasta in Siskiyou County (Griffin and Critchfield, 1972).

Crataegus columbiana: This is disjunct by about 300 km to the south of the nearest known populations on the Modoc Plateau, northeastern California.

Townsendia scapigera: Populations at Carson Pass are separated by 65 km from nearby stations in the Virginia Range, Nevada, and the Sweetwater Mountains, Mono County, California.

Table 1. Disjunct Taxa from the Great Basin in the Alpine and Subalpine Zones at Carson Pass.

Trees

Pinus monophylla, Betula occidentalis

Shrubs

Amelanchier utahensis, Artemisia arbuscula, A. tridentata ssp. *vaseyana, Cercocarpus ledifolius, Chrysothamnus nauseosus* ssp. *albicaulis, C. viscidiflorus, Crataegus columbiana, Eriogonum microthecum, Purshia tridentata, Ribes velutinum, Rosa woodsii* var. *ultramontana, Tetradymia canescens*

Herbs

Antennaria dimorpha, Allium parvum, Agoseris glauca var. *monticola, Aster adscendens, Astragalus purshii* var. *lectulus, A. whitneyi, Brickellia oblongifolia* var. *linifolia, Balsamorhiza sagittata, Cirsium utahense, Chenopodium overi, Crepis acuminata, C. bakeri, C. modocensis* ssp. *subacaulis, Castilleia linariaefolia, Chamaesaracha nana, Erigeron aphanactis, E. linearis, E. nevadincola, E. tener, E. eatonii* ssp. *plantagineus, E. breweri* var. *porphyreticus, Haplopappus acaulis, H. bloomeri, Hydrophyllum capitatum* var. *alpinum, Leptodactylon pungens* ssp. *pulchriflorum, Lupinus caudatus, Lygodesmia spinosa, Melica stricta, Mentzelia dispersa, Mimulus densus, Navarretia breweri, Poa cusickii, P. juncifolia, P. nevadensis, Phoenicaulis cheiranthoides, Phacelia humilis, Phlox covillei, Senecio canus, Scrophularia desertorum, Townsendia scapigera, Viola beckwithii, Zigadenus paniculatus*

Xeric Vegetation

The disjunct taxa (Table 1) are largely restricted to dry, rocky or shallow soil sites at Carson Pass, where they contribute to two distinctive associations, both of which have admixtures of Great Basin and Sierran elements.

Sites at lower elevations (2500–2700 m) on southerly or easterly exposures with slightly acid soils (pH 5.6–6.4) support an open woodland (< 50% canopy coverage) of *Juniperus occidentalis* ssp. *australis,* with scattered *Populus tremuloides* and *Pinus contorta* var. *murrayana.* The associated low shrub layer (< 1 m) is composed of *Artemisia tridentata* ssp. *vaseyana, Ribes cereum, Symphoricarpos vaccinioides, Chrysothamnus nauseosus* ssp. *albicaulis, Holodiscus microphyllus,* and *Ceanothus cordulatus* along with perennial herbs such as *Wyethia mollis, Balsamorhiza sagittata,* and *Erigeron breweri* var. *porphyreticus.* This *Juniperus occidentalis* ssp. *australis/Artemisia tridentata* ssp. *vaseyana* association is found on fairly deep (1.0–1.2 m), well-drained soils derived from granitic or coarse-grained volcanic parent materials (Rogers, 1974). Snow cover is nearly continuous from November to late April, and adequate soil moisture is available until early summer.

The second association inhabits higher elevations (2600–3000 m) on nearly neutral (pH 7.0–7.8), shallow (< 0.5 m), rocky soils derived from volcanic rocks. This low (< 0.5 m tall) vegetation is composed chiefly of the shrubs *Artemisia arbuscula, Haplopappus acaulis, Leptodactylon pungens* ssp. *pulchriflorum, Amelanchier utahensis,* and *Tetradymia canescens.* The numerous perennial herbs in this association contribute little to the sparse ($< 25\%$) cover. This *Artemisia arbuscula/Haplopappus acaulis* association occupies the driest, most wind-exposed sites. Snow cover is intermittent to nearly absent in winter, and water availability is low through the year.

In overall physiognomy, structure, or composition these two associations are strikingly similar to the *Pinus monophylla/Juniperus osteosperma* woodland and *Artemisia tridentata* scrub vegetation types of the Great Basin, such as those described by Daubenmire (1971) and Franklin and Dyrness (1973) for eastern Washington, by Lewis (1971) and Loope (1969) for the Ruby-East Humboldt Mountains of eastern Nevada, and by Blackburn et al. (1968, 1969), Billings (1945, 1951), and Beeson (1974) for central Nevada. Some of the stands described by Daubenmire and located 1000 km to the north are nearly identical in composition to stands at Carson Pass.

Migrational History

Members of the Great Basin floristic element at Carson Pass are almost exclusively limited to the vegetation types described above. The question arises as to when and how these disjunct communities came to occupy azonal sites in the northern Sierra Nevada.

There is low probability that each of the disjunct taxa was dispersed to Carson Pass independently, subsequently reconstituting a disjunct phytosociological assemblage; rather, it is more likely that they migrated as an intact vegetation unit.

These disjunct communities are currently isolated from similar neighboring populations by expanses of mesic forest and meadow vegetation. The thesis advanced here is that these communities migrated to Carson Pass and into other areas west of the Sierran crest when past climate was significantly different from that of the present. Subsequent climatic changes have forced their general restriction to the east, leaving relict patches on compensatory, azonal sites.

The course of climatic change for North America since the last glacial epoch of the Pleistocene is fairly well documented in the literature, although data for California are scarce. Full glacial climates were cooler than at present by 8–9°C mean annual temperature (MAT) (Wright and Frey, 1965; Flint, 1973) and had lower evapotranspiration rates resulting in greater moisture availability, although overall precipitation may have been reduced as much as 10–15 percent (Galloway, 1970). A gradual warming trend began at the close of the last ice advance, 12,000–14,000 years B.P., and continued until approximately 3500 years B.P., followed by a minor cooling trend up to the present. The intermediate period of warming (termed the Xerothermic period) extended from about 6600–3500 years B.P. and was characterized by reduced precipition and by MAT's 3–5°C higher than at present.

Comparison of climatic characteristics of selected weather stations in

TABLE 2. COMPARISON OF THE CLIMATIC CHARACTERISTICS OF SELECTED STATIONS REPRESENTING UPLAND VEGETATION TYPES OF NEVADA WITH THE TWIN LAKE STATION AND THE INFERRED CLIMATE OF THE ARTEMISIA ARBUSCULA/HAPLOPAPPUS ACAULIS ASSOCIATION AT CARSON PASS. MAT = mean annual temperature; AR = annual range of mean monthly temperatures; TW = mean monthly temperature warm month; TC = mean monthly temperature cold month; PPT = precipitation. Values are in °C and mm of water; data from report by U. S. Department of Commerce (1972).

Station	MAT	AR	TW	TC	PPT
Carson Pass					
Artemisia arbuscula/Haplopappus acaulis scrub					
Twin Lakes (projected)	3.1	16.1	12.3	—3.8	655
Pinus contorta var. *murrayana* forest-*Carex/Salix* meadow					
Twin Lakes	3.9	17.6	12.8	—4.8	1180
Nevada					
Pinus monophylla/Juniperus osteosperma woodland					
Austin	8.6	22.6	21.2	—2.0	302
Contact	8.0	23.6	20.6	—3.0	212
Elko	7.4	26.0	20.8	—5.2	230
Ely	6.9	24.8	19.7	—5.1	212
Wells	7.1	25.8	20.7	—5.1	243
Virginia City	8.8	21.2	21.6	—0.7	265
Lehmann Caves	8.6	23.1	21.7	—1.4	324
Artemisia tridentata scrub					
Reno	9.1	20.4	19.8	—0.8	182
Battle Mountain	8.6	25.1	21.8	—3.3	176
Minden	9.8	21.4	20.8	—0.6	219
Carson City	10.0	20.9	20.9	0.0	282

Nevada with records from the Twin Lakes (Caples Lake) station at Carson Pass is given in Table 2. The Twin Lakes station is located in an open, seasonally wet meadow covered with clones of *Salix lemmonii* interspersed in a matrix of *Carex rostrata, C. nebrascensis, C. aquatilis,* and *Deschampsia caespitosa* surrounded by closed-canopy forest of *Pinus contorta* var. *murrayana.* Temperature records collected by me during 1971–1974 for a nearby locality (1.5 km northwest of the Twin Lakes station) dominated by *Artemisia arbuscula* and *Haplopappus acaulis* are slightly cooler by an average of 1°C, although comparable to the values for the Twin Lakes station. Precipitation falling as snow on the dry, windswept slopes dominated by the *Artemisia/Haplopappus* association where many of the disjunct taxa occur is reduced by 50–70 percent of that recorded at the Twin Lakes station. The climate given for the *Artemisia/Haplopappus* association is inferred from the Twin Lakes long-term record by taking this precipitation loss into account. The MAT at Twin Lakes is 3.9°C, with an annual range of mean monthly temperatures (AR) of 17.6°C. Temperatures given in Table 2 for the *Artemisia/ Haplopappus* association are lapse-rate projections from the Twin Lakes station based on 4 years of record. Great Brasin stations shown in Table

2 have MAT values from 6.9 to 10.0°C. and AR values from 20.4 to 26.0°C. An increase of 4–5°C in MAT (without significant changes in AR) and lowered precipitation during the Xerothermic Period would produce a climate at Carson Pass more similar to the present climate of the Great Basin and could account for the observed disjunctions. Comparison of the annual water balance (Thornthwaite, 1948; Black, 1966) at the Twin Lakes station and the inferred water balance for the *Artemisia/Haplopappus* association at Carson Pass with selected stations in Nevada is given in Table 3. The annual water balance for the *Artemisia/Haplopappus* association assumes mean monthly temperatures 1.0°C cooler than the Caples Lake station, with 50 percent of the precipitation falling as snow lost as a result of wind redistribution and deflation of the snowpack and 50 mm of soil water storage. Regimes for the Twin Lakes station at Carson Pass and the Nevada stations assume a soil water storage of 100 mm. Also given in Table 3 is the inferred regime of the *Artemisia/Haplopappus* habitat at Carson Pass with a Xerothermic MAT of 4°C higher than at present, reducing zonal precipitation 20 percent, with the same loss of snow-derived moisture and the same soil

Table 3. Comparison of the Present Annual Water Balance Regime of the Artemisia/Haplopappus Association, the Twin Lakes Station at Carson Pass, and Selected Stations Representing Upland Vegetation Types of Nevada with the Inferred Xerothermic Water Balance of the Artemisia/Haplopappus Habitat at Carson Pass. PE = potential evapotranspiration; AE = actual evapotranspiration; WS = snowmelt run-off; WD = annual water deficit. Values are in mm of water. All calculations assume 100 mm of soil water storage except those for the *Artemisia/Haplopappus* association.

Station	PE	AE	WS	WD
Carson Pass				
Artemisia arbuscula/Haplopappus acaulis scrub				
Twin Lakes (projected)	451	222	433	229
Twin Lakes Xerothermic (+4°C MAT)	564	252	384	312
Pinus contorta var. *murrayana* forest-*Carex/Salix* meadow				
Twin Lakes	471	283	897	188
Nevada				
Pinus monophylla/Juniperus osteosperma woodland				
Austin	601	269	33	333
Contact	598	212	0	387
Elko	590	222	8	369
Ely	567	212	0	356
Wells	580	212	31	368
Virginia City	588	214	51	374
Lehmann Caves	604	285	39	319
Artemisia tridentata scrub				
Reno	619	182	0	437
Battle Mountain	616	176	0	440
Minden	635	212	8	428
Carson City	641	215	67	426

water storage. The inferred Xerothermic water balance regime and climate for the driest sites at Carson Pass are very similar to present day conditions at upland sites in the Great Basin.

A warmer climate during the Xerothermic period would be favorable to migration of Great Basin elements into the central Sierra Nevada west of the crest. Warmer, south-facing or east-facing slopes with their characteristically shallow soils would be the most accessible habitats for Great Basin vegetation. Xeric vegetation types present at Carson Pass may therefore be relicts of Xerothermic expansion of Great Basin vegetation westward and upward into the Sierra Nevada. They appear to have persisted in compensatory sites where competition from more mesic forest and meadow vegetation is reduced.

Detling (1953, 1958, 1961) and Hickman (1968) presented evidence for a similar Xerothermic intrusion of xeric vegetation from eastern and southern sources into mesic areas of western Oregon. Similarly, Great Basin elements from the volcanic plateaus of Modoc and Siskiyou counties extended into the high mountains of the North Coast Ranges during the Xerothermic. Taxa such as *Artemisia arbuscula, Symphoricarpos vaccinioides, Arenaria congesta, Purshia tridentata, Crepis acuminata, Erigeron eatonii, Paeonia brownii, Allium parvum, Astragalus purshii* var. *lectulus,* and *Leptodactylon pungens* ssp. *pulchriflorum* are recorded from azonally dry sites in the Klamath-Trinity region (Ferlatte, 1974; Muth, 1967; Ground, 1972). Axelrod (1966) identified a parallel Xerothermic expansion of warm desert vegetation into coastal southern California and the South Coast Ranges.

A Xerothermic expansion hypothesis cannot explain the disjunction of all Great Basin plants known to occur in cismontane areas of California, however. Elements of *Pinus monophylla/Juniperus californica* woodland extend westward well into the South Coast and Transverse ranges in southern California (see Axelrod, 1966, p. 50). *Artemisia tridentata* occurs in the hills surrounding Coalinga, in the inner South Coast Ranges of Fresno County at elevations of 400–700 m (Weiler, 1966). These distributions were undoubtedly achieved during the last full-glacial period, as evidenced by macrofossils of *Pinus monophylla* and *Juniperus californica* in oil-seeps on the floor of the San Joaquin Valley at McKittrick, Kern County (Mason, 1944) dated at 38000± 2500 radiocarbon years B.P. (Berger and Libby, 1966). *Pinus monophylla* is found in several scattered locations at mid-elevations on the west slope of the Sierra Nevada. The Kings River population described by Howell (1961) from near Tehipite Valley is found on dry, rocky, south-facing slopes amidst montane chaparral vegetation and is associated with other Great Basin taxa including *Cercocarpus intricatus, Artemisia tridentata, Carex filifolia, Stipa speciosa, Phacelia cryptantha,* and *Eriogonum saxatile* and with the desert elements *Yucca whipplei* and *Garrya flavescens* var. *pallida.* Similar sites in the Tuolumne River canyon at Hetch Hetchy support *Pinus monophylla, Chrysothamnus* *nauseosus* ssp. *albicaulis, Artemisia tridentata,* and *Erigeron breweri.* Harwell (1937) felt these west slope locations for *Pinus monophylla* represented aboriginal introductions, but this seems less likely when the number of associated disjuncts is considered. A more likely explanation would have these populations established in the late Pleistocene by migration without human assistance along the western foothills of the Sierra Nevada from populations known to exist in the southern San Joaquin Valley at the time (Mason, 1944).

The wide amplitude of climatic fluctuations during the late Pleistocene must have had a large effect on the abundance of organisms (Wright and Frey, 1965; Flint, 1973). The disjunction of the Great Basin floristic element at high elevations on the west slope of the northern Sierra Nevada is best explained by a westward expansion during the warm, dry Xerothermic Period.

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THE BIGCONE DOUGLAS-FIR—CANYON LIVE OAK COMMUNITY IN SOUTHERN CALIFORNIA

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Little is known about the ecology of bigcone Douglas-fir [*Pseudotsuga macrocarpa* (Vasey) Mayr]. Its relations to tree associates, soils, topography, and habitat are at best poorly understood. Whether or not bigcone Douglas-fir occupies a dominant or subordinate position within its habitat is not well known. Is it regenerating and invading new areas vigorously, holding its own, or losing ground?

Various workers have described the location, silvics, and habitat of bigcone Douglas-fir. Mason (1927) included bigcone Douglas-fir in his California Coast Range Forest, considering it an endemic and relict species. Sudworth (1908) described the natural range of the species as being delimited by lack of moisture at low elevations and by severity of climate at high ones. Furthermore, the species grows on sites too shallow, rocky, or dry for most other conifers.

In his study of vegetational types of the San Bernardino Mountains, Horton (1960) considered bigcone Douglas-fir to be a member of two vegetation types: (1) a Live Oak Woodland and (2) a bigcone Douglas-fir type. The Live Oak Woodland type usually is found on north slopes, where canyon live oak (*Quercus chrysolepis* Liebm.) predominates, although scattered individuals of bigcone Douglas-fir are often found. Bigcone Douglas-fir dominates in its type, but canyon live oak usually is present. Dominance of bigcone Douglas-fir often is reduced by fire. "Those portions of the bigcone Douglas-fir forest that are destroyed are